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SHORT COMMUNICATION

Scopulate hairs in male *Liphistius* spiders: probable contact chemoreceptors

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Abstract. Adult male *Liphistius* have dense hair pads on the ventral side of their tarsi. At first glance they appear like the adhesive scopulae, which are well known from mygalomorph spiders. However, a fine structural analysis of these scopulate hairs shows that they lack the brush-like structure with tiny "endfeet" that is typical for such adhesive hairs. Instead, the smooth hair shaft exhibits a small pore ventrally, about 8–10 µm from the blunt tip. A thin cuticular canal extends from that pore through the middle of the hair shaft and terminates about 30 µm above the hair base. Transmission electron mieroscopy reveals that this central canal contains about 16 delicate dendrites. The morphology of these scopulate hairs thus corresponds closely to contact chemoreceptors known from other spiders. Since these scopulate hairs occur only in adult males, they are likely involved in the perception of female pheromones.

Keywords: Morphology, scopulae, Mesothelae

Many wandering spiders possess dense hair pads (scopulae) on the ventral side of their tarsi. Such scopula hairs have a brush-like appearance, and they serve to enhance adhesion to the substrate (Homann 1957; Hill 1977; Foelix 1985a; Kesel et al. 2003). With the aid of the distal-most hair pad (claw tuft), spiders can move sure-footedly on smooth, vertical surfaces. The more extensive hair pads on the proximal tarsus (and often metatarsus) are not involved in walking, but enable a spider to achieve a firm grip on its prey (Rovner 1978; Foelix et al. 1984). The ancient mesothele spiders in the genus *Liphistius* also exhibit tarsal "scopulae," but only in the adult males. A eloser inspection with the scanning electron microscope showed that the structure of these scopulate hairs is quite different from the regular adhesive hairs (Foelix & Erb 2010). Their hair shaft is rather smooth and lacks the many flared extensions ("end feet") that provide the contact points for adhesion (Foelix & Chu-Wang 1975; Niederegger & Gorb 2006). The question now was what the function of these scopulate hairs in *Liphistius* might be, if adhesion could be ruled out. Since these hairs occur only in adult male spiders, it seemed likely that they are somehow involved with pheromones. They could either produce a male secretion (pheromone) that would act as a signal for the female, or these hairs could be chemoreceptors that would perceive the female pheromone. In order to solve this question, we inspected the scopulate hairs of male *Liphistius* spiders with transmission (TEM) and scanning electron microscopes (SEM). In particular, the examination of thin sections in the TEM should provide an answer as to whether these hairs are assoeiated with glandular or with sensory cells.

Whole mounts of isolated "scopulae" fragments from male *Liphistius desultor* Schiödte 1849 and *L. endau* Sedgwick & Platnick 1987 were used for light microscopy. Phase contrast was best suited for revealing the internal structure of scopulate hairs.

For SEM, we dehydrated alcohol-fixed material in a series of ethanol and acetone, then transferred it to HMDS (hexamethyldisilazane) for 15 min before air-drying on filter paper. Tarsi were mounted ventral side up on carbon-coated stubs, sputtered with gold, and examined in a Zeiss DSM 950 SEM.

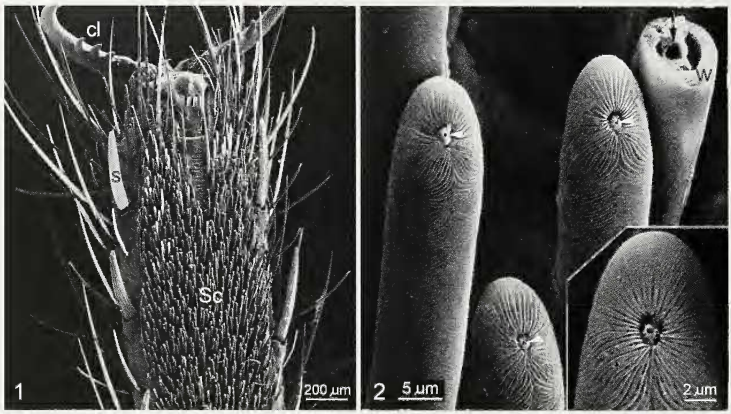
For TEM, tarsi from a male *Liphistius dangrek* Schwendinger 1996 were cut into small pieces, fixed in cold 5% cacodylate-buffered glutaraldehyde for 20 h, and post-fixed in 1% OsO_4 for 2 h. After dehydration in ethanol and propylene oxide, specimens were infiltrated with hard Epon overnight and then flat embedded and polymerized at 65° C. We then cut thin sections with a diamond knife, picked them up on Formvar-coated copper grids where they were contrasted with uranyl acetate and lead citrate for 10 min each. A Zeiss 9S2 and a JEOL TEM-1011 were used for fine structural examination.

The scopulate hairs in male *Liphistius* occur on the ventral tarsi, but not on the metatarsi. There is a marked difference in the number of these hairs between the different legs. Whereas the tarsi of the first pair of legs have only a distal hair pad of 150–200 hairs, the tarsi of the hind pair of legs are densely covered with 1,500–2,000 hairs.

Each tarsal hair pad is flanked laterally by a row of 6–8 curved spines (Fig. 1). A few tactile hairs are arranged serially in the midline of the hair pad, but there is no distinct division into two stripes as is the case in the scopulae of certain mygalomorphs.

Scopulate hairs are between 130–160 µm long and 10–14 µm in diameter (Figs. 2, 3). The base of the hair shaft is movably inserted into a socket (Fig. 4), and the distal end is blunt and slightly curved toward the leg surface. At low magnification the hair shaft appears smooth, but at higher magnification (SEM) shows fine ridges running perpendicular to the hair axis. Near the round tip of the hair, these ridges converge toward a small pore of 0.3–0.4 µm diameter (Fig. 2). This pore is always located subterminally, about 8–10 µm away from the tip, on the ventral side. While the pore opening is easily seen with the SEM, it is hardly detectable in the light microscope. However, under phase contrast microscopy, a thin central canal is visible inside the hair shaft, which begins at the distal pore, traverses the center of the hair shaft and terminates about 30 µm above the hair base (Figs. 3, 4).

Cross-sections of scopulate hairs show a solid, thick wall (2–3 µm) and a lymph-filled lumen (Fig. 5). The cuticular central canal has a much thinner wall (about 0.5 µm) and is filled with a rather dense lymph (Figs. 5, 6). More importantly, this central canal encloses many fine nerve fibers. The average number of these dendrites is 16, rarely 18–20. Their diameter is only 0.1–0.2 µm, and each dendrite contains only a few microtubules (2–9; Fig. 7). Closer to the hair base

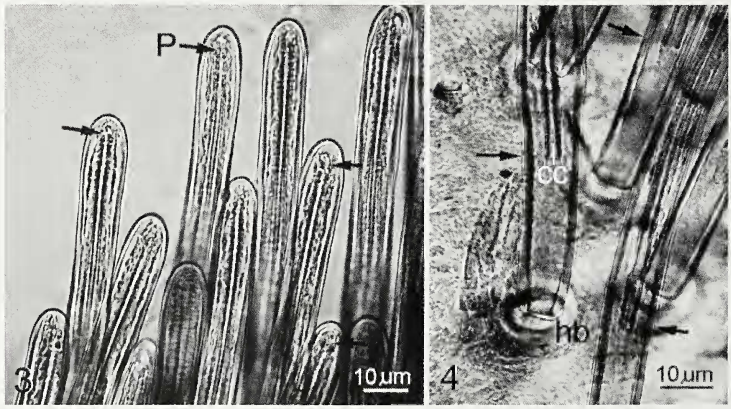


Figures 1, 2.—Ventral side of a tarsus in a male *Liphistius endau*. 1. The dense pad of scopulate hairs (Sc) is flanked by stout spines (S). Two main claws (cl) and a short middle claw (m) are seen on top. 2. Close-up of several scopulate hairs, ventral view. The hair shaft bears fine cuticular ridges, which converge toward a small, subterminal pore (arrow heads). One hair shaft is broken and reveals a rather thick hair wall (w) and a circular central canal (arrow) in the lumen. *Inset*: Pore and cuticular ridges at higher magnification.

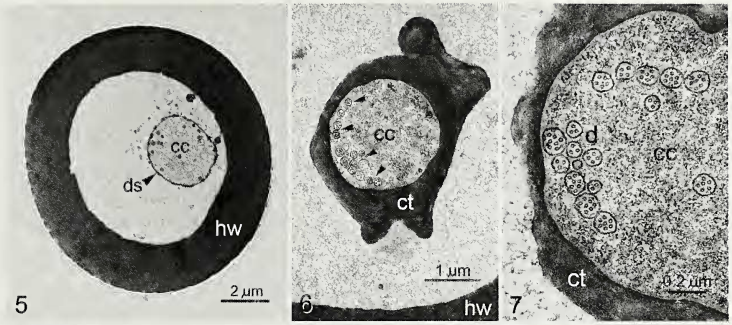
where the central canal ends (Fig. 4), the dendrites are encased by a very thin layer of extracellular material, the dendritic sheath (Fig. 5). At present we do not know yet whether there are any dendrites terminating at the base of the hair shaft, which would indicate an additional mechanoreceptive function.

Considering that there are at least 16 sensory cells per scopulate hair and the fact that one tarsus may be covered by 1,500–2,000 scopulate hairs (Fig. 8), there must be an enormous number of sensory nerve fibers in each tarsus. Indeed, cross-sections of a tarsus show two substantial sensory nerves (Fig. 9), but the exact number of nerve fibers (axons) cannot be determined in the light microscope due to their small diameter (mostly 0.1–0.2 µm). However, a few large axons of more than 10 µm in diameter can be seen with the light microscope (Fig. 10). They are reminiscent of the giant fibers known from other ancient arachnids e.g., in amblypygids (Foelix 1975). However, further studies using TEM are needed to confirm the presence of such giant fibers and associated synaptic connections.

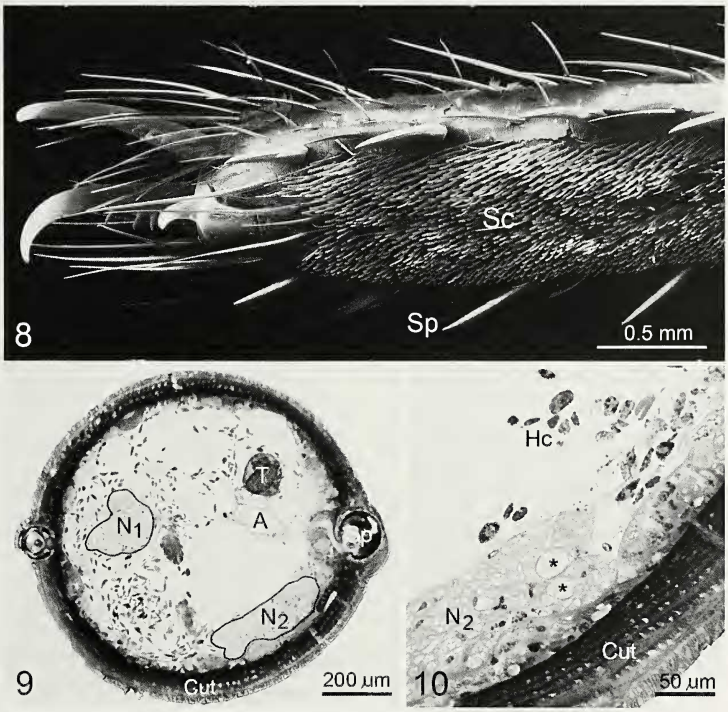
Finally, it was brought to our attention (Schwendinger pers. comm.) that "scopulae" restricted to adult males also occur in certain mygalomorph spiders (e.g., among the Idiopidae). For comparison we looked at one representative, *Idiops pylorus* Schwendinger 1991, and found very similar tarsal hair pads as in *Liphistius* (Fig. 11). Again, these scopulate hairs lack the highly branched structure of the common scopula (adhesive) hairs, and the smooth hair shaft bears the



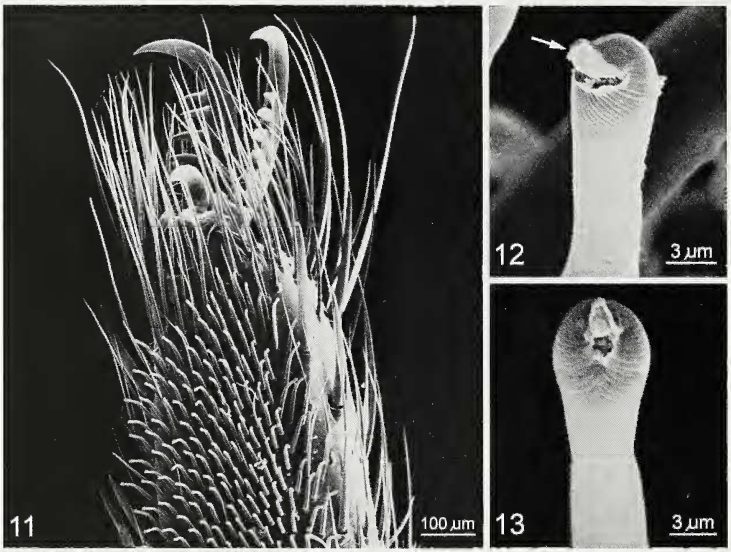
Figures 3, 4.—Scopulate hairs from a male *Liphistius desultor*, as seen in a wholemount. 1. The hair shaft contains a central canal that terminates in a small pore (P, arrows) just before reaching the blunt tip of the hair. 4. The basal region of scopulate hairs exhibits a distinct socket at the hair base (hb) and the beginning central canal (cc) about 30 µm above the hair base (arrows).



Figures 5–7.—Cross-sections of scopulate hairs. 1. In basal region, the hair wall (hw) is relatively thick, while the central canal (cc) is enclosed by a thin dendritic sheath (ds). The fine nerve fibers inside the central canal are barely visible at this low magnification. 6. In midregion the hair shaft shows that the dendritic sheath has been replaced by a massive cuticular tube (ct). Small nerve fibers (arrowheads) are apparent in the left half of the central canal (cc). 7. High magnification of the central canal (cc) reveals about 16 small dendrites (d) containing 2–9 microtubules each. Note the different density of the hemolymph inside and outside of the central canal (cc).



Figures 8–10.—8. Tarsus 4 in a male *Liphistius desultor*, ventrolateral view. About 800 scopulate hairs (Sc) were counted on this distal portion; the entire tarsus contains about 1,750 of these sensory hairs. Sp = lateral spine. 9. Cross-section of a tarsus in *Liphistius dangrek*. The hair bases of two spines (Sp) are located laterally in the thick leg cuticle (Cut). Two sensory nerves (N_1, N_2) comprise the axons of all the tarsal sensory hairs. A = leg artery, T = tendon of claw muscles. 10. Detail of a cross-sectioned sensory nerve (N_2) showing many small axons and two "giant fibers" (asterisks) of more than 10 µm in diameter. Hc = hemocytes (blood cells).



Figures 11–13.—Tarsus of a male *Idiops pylorus*. 11. Ventro-lateral view. Note the pad of scopulate hairs directly below the three tarsal claws. 12. The tip of these scopulate hairs shows an overhanging cuticular hood (arrow) that conceals the pore underneath. 13. A straight ventral view of the hair tip reveals the pore opening under the tongue-like hood.

same delicate ridges. The only morphological difference is that the subterminal pore opening is covered by a cuticular flap or hood (Figs. 12, 13).

There are two remarkable features about the scopulate hairs in *Liphistius* : 1) these hairs differ from the common adhesive hairs of scopulae found in other spiders (e.g., in tarantulas), and 2) these scopulate hairs occur only in the adult male spiders but not in females or juveniles.

The structure of these scopulate hairs is very similar to known contact chemoreceptors in arthropods, especially in spiders (Foelix 1985a). The most convincing evidence for chemoreception is the presence of numerous small dendrites lying inside the hair shaft; most likely, they are exposed to the environment at the pore opening below the tip. The number of dendrites is similarly high (16), as in the regular chemosensitive hairs of spiders (19) (Foelix 1970; Foelix & Chu-Wang 1973; Harris & Mill 1973). It is noteworthy that the "regular," S-shaped taste hairs are also present in *Liphistius*, usually in rows on the dorsal side of the tarsus but also interspersed among the hundreds of ventral scopulate hairs. Perhaps those regular taste hairs are more generalized chemoreceptors, whereas the scopulate hairs are more specialized (e.g., for the detection of female pheromones). This interpretation is supported by the fact that scopulate hair pads occur only in adult male spiders. Indirect support comes from behavioral observations: males can apparently differentiate trap doors from receptive females and from juveniles – only the former are approached during courtship, whereas the latter are ignored (Haupt 2003).

The exclusive occurrence of scopulate hairs in the male is not restricted to *Liphistius* species, but has also been noted in several mygalomorph families; e.g., in Actinopodidae, Antrodiaetidae, Atypidae, Ctenizidae, Cyrtaucheniidae, and Idiopidae (Raven 1985). Indeed, in *Idiops pylorus*, we have found the same type of scopulate hairs as in *Liphistius* (Figs. 11–13). This widespread occurrence indicates that the presence of scopulate hairs may be an ancient (plesiomorphic) character that is shared by the Mesothelae and many Mygalomorphae. Until now these scopulate hairs have not been reported in the literature on Mesothelae (Haupt 2003); in Mygalomorphae they were only used for classification, but without any indication of their possible function (Raven 1985).

A remaining question is why a male spider would need several thousands of such scopulate hairs. We counted about 1,750 scopulate hairs on a single tarsus (leg 4), which corresponds to 28,000 nerve fibers just for the sensory input of scopulate hairs from one leg. This is even more than the entire sensory input found in the antenniform legs of amblypygids (about 20,000 nerve fibers; Foelix & Troyer 1980; Foelix et al. 2002). It seems that *Liphistius* also has a similar system of giant fibers (Fig. 10) and associated synapses, as was found in amblypygids and other arachnids (Foelix 1975, 1985b; Fabian-Fine et al. 2000, 2002), but this needs to be clarified with further ultrastructural studies.

Finally, the extremely high sensory input from thousands of chemoreceptors is also baffling when we consider the short time span during which it can actually be used: adult *Liphistius* males die only a few weeks after their final molt (Schwendinger pers. comm.); perhaps the wandering males need to optimize the chance of finding a female during that brief time.

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